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Combining Ability of Female Channel Catfish, *Ictalurus punctatus*, and Male Blue Catfish, *I. furcatus*, for Early Growth Performance of Their Progeny †

Ramjie Odin [1,2,*], Ahmed Elaswad [1,3], Karim Khalil [1,4,5], Khoi Vo [1], Nathan J. C. Backenstose [1,6], Zachary Taylor [1], David Drescher [1,7], William S. Bugg [1,8], Dalton Robinson [1], Kamal Gosh [1,9], Zhi Ye [1,10,11], Guyu Qin [1,12], David Creamer [1] and Rex Dunham [1,*]

1 School of Fisheries, Aquaculture, and Aquatic Sciences, Auburn University, Auburn, AL 36849, USA; a.elaswad@squ.edu.om (A.E.); karim.khalil@vet.cu.edu.eg (K.K.); kmv0005@yahoo.com (K.V.); njbacken@buffalo.edu (N.J.C.B.); zachtaylor8492@gmail.com (Z.T.); ddrescher132@gmail.com (D.D.); wbugg@mail.ubc.ca (W.S.B.); dalton.a.robinson@gmail.com (D.R.); kgosh@langston.edu (K.G.); yezhi@ouc.edu.cn (Z.Y.); gzq0002@auburn.edu (G.Q.); davidandrewcreamer@gmail.com (D.C.)
2 College of Fisheries, Mindanao State University-Maguindanao, Datu Odin Sinsuat 9601, Philippines
3 Center of Excellence in Marine Biotechnology, Sultan Qaboos University, Muscat 123, Oman
4 Anatomy and Embryology Department, Faculty of Veterinary Medicine, Cairo University, Giza 12211, Egypt
5 Department of Veterinary Medicine, College of Applied & Health Sciences, A'Sharqiyah University, Ibra 400, Oman
6 Department of Biological Sciences, State University of New York at Buffalo, Buffalo, NY 14228, USA
7 Department of Fisheries, Muckleshoot Indian Tribe, 39015-A 172nd Ave SE, Auburn, WA 98092, USA
8 Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2M5, Canada
9 Department of Agriculture and Natural Resources, Langston University, Langston, OK 73050, USA
10 MOE Key Laboratory of Marine Genetics and Breeding, College of Marine Life Sciences, Ocean University of China, Qingdao 266003, China
11 Key Laboratory of Tropical Aquatic Germplasm of Hainan Province, Sanya Oceanographic Institution, Ocean University of China, Sanya 572000, China
12 Division of Cardiovascular Medicine, Stanford University, Palo Alto, CA 94305, USA
* Correspondence: ramjieodin@msumaguindanao.edu.ph (R.O.); dunhara@auburn.edu (R.D.)
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Abstract: The hybrid between the female channel catfish (*Ictalurus punctatus*) and the male blue catfish (*I. furcatus*) is the best genetic type currently available for commercial catfish farming due to their superior traits. However, further genetic improvements can be achieved by selecting parents with increased combining abilities. Twenty female channel catfish and twelve male blue catfish were crossed in a partial factorial mating design, resulting in forty hybrid families. These families were evaluated for early growth in three different rearing systems, including ponds and aquaria. The early growth performance of hybrid catfish was significantly ($p < 0.05$) affected by the additive gene action of the female parent and the male parent. There were genotype–environment or genotype–age interactions affecting the combining abilities, both the amount and the type of genetic variation. Dam GCA was significant in all environments/ages; however, sire GCA was variable, and SCA was not significant. These findings suggest that reciprocal recurrent selection for growth could potentially improve the performance of F1 hybrid catfish.

Keywords: hybrid catfish; combining ability; genetic variance component; GCA; SCA

Key Contribution: This study revealed that the early growth performance of channel–blue hybrid catfish is significantly influenced by the additive gene action of the female parent and male parent. This finding could potentially lead to more effective breeding strategies for hybrid catfish.

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1. Introduction

Catfish has been the leading aquaculture commodity in the US for approximately 4 decades. However, US catfish production has declined from its peak production in 2003 because of rising production costs and the failure to compete with imported cheap catfish, resulting in a significant decrease in the number of catfish farms and US catfish sales [1].

The hybrid catfish from crossing female channel catfish and male blue catfish (C×B) can help address the problems of the catfish industry. Hybrid catfish have faster growth [2–10], better FCR [3,9], higher tolerance to low dissolved oxygen [11], increased bacterial disease resistance diseases [6,12–14], uniformity in size and shape [3,15–17], high dress-out percentage and fillet yield [8,18–22], increased harvestability [3,19,23], and angling vulnerability [24,25] compared to the parent species.

Currently, a small number of catfish hatcheries produce most of the hybrid fingerlings, which are sold to numerous independent grow-out catfish farmers [26]. Approximately 70% of catfish production and processing is hybrid catfish in the US catfish industry (Nagaraj Chatakondi, Syndel, Ferndale, WA, USA, personal communication). The hybrid catfish is not a panacea. Not all hybrids perform equally, and the performance of hybrid catfish varies due to parental strain and individual genetic effects [4,21,27–29]. This genetic variability is an opportunity to genetically improve the interspecific hybrid.

Reciprocal recurrent selection, which is the selection of purebred parents based on the hybrid progeny performance, offers great promise to genetically improve the desirable traits of hybrid catfish. To achieve this purpose, information about the combining ability of the parents and their performance in hybrid combination is a prerequisite to developing the most efficient and effective breeding plans [30]. Griffing [31] proposed the partition of the total genetic variation into general combining ability (GCA) of the parents and specific combining ability (SCA) of the crosses, defining GCA as the average performance of the parental lines in hybrid combinations an SCA as the performance of a combination of parents in a specific cross. The estimation of GCA and SCA has been widely used for developing corn breeding programs and has been applied to various breeding programs for plants and animals, including fish [26,32–40]. However, there are very few analyses of GCA and SCA for economic traits of catfish, such as growth and carcass yield of market-size F1 hybrid catfish [26,40], oxygen tolerance [39], and resistance to enteric septicemia in channel catfish [32].

Bosworth and Waldbieser [26] reported that the GCA of the parental dam was more important in controlling the carcass yield and harvest weight of F1 channel–blue hybrids. Similarly, GCA was also found to be important in the expression of traits pertaining to the tolerance of hybrid catfish to low dissolved oxygen [39], hardness, chewiness, and gumminess of hybrid catfish meat quality [40] and resistance to enteric septicemia in Norris and Marion x Kansas strains of channel catfish [32]. On the other hand, SCA was found to influence the hybrid catfish fillet yield, resilience, springiness, and yellowness [40]. These results suggest the potential of combining ability estimation for selection to improve the desired traits of catfish.

Combining ability estimation is considered a useful criterion for selecting elite parents. General and specific combining abilities are important indicators for the potential catfish parents to produce consistently better performing F1 hybrid catfish. GCA and SCA variances estimate the additive and non-additive gene actions, respectively [41].

Although the channel–blue hybrid catfish is genetically superior to the parent species, it could be further improved for growth rate. Additionally, a recent industry problem is variable growth by hybrids, and a partial solution to that problem could be from genetic selection. To determine the potential for genetically improving these traits for hybrid catfish, the combining abilities of the parent species must be estimated. No research has been conducted yet to determine and estimate the combining abilities for early performance traits of F1 hybrid catfish.

The objectives of this research were to estimate the GCA and SCA for the early growth performance of female channel catfish × male blue catfish F1 hybrid progeny in terms

of body weight. Additionally, the individual combining abilities of the parents were determined. The genetic variance components for early growth of hybrids during an initial 311 days of tank rearing in a flow-through system and after an additional 245 days of tank rearing in a recirculating system and communal rearing in a split pond were determined. The best parental genotypes with high GCA and the best parental cross with high SCA that produce superior-performing hybrid catfish were identified. This research will be beneficial to improving the selection and breeding programs for hybrid catfish production.

2. Materials and Methods

2.1. Experimental Fish

Twenty females from nine strains of channel catfish were crossed with twelve males from four strains of blue catfish [42] to produce F1 C×B hybrid catfish progeny. The nine strains of female channel catfish were Tishomingo, AR, Kansas Select, Kansas Random, ARMK, Kansas × Thompson, Rio Grande, Thompson, and mixed strains. The four strains of male blue catfish were D&B, Rio Grande, D&B × Rio Grande, and Tombigbee. These fish were maintained at the Fish Genetics Unit, E.W. Shell Fisheries Research Center, Auburn University, Alabama. All procedures involving the handling and treatment of fish in this study were approved by the Auburn University Institutional Animal Care and Use Committee (AU-IACUC).

The twenty channel catfish females (dams) were from nine strains. The strains used included Kansas Random (KR), which originated from Ninnescah River in 1911 and is the oldest domestic strain of channel catfish [42]. This strain was randomly bred and has the traits of increased resistance to disease, rapid growth, and late sexual maturity. Kansas Select (KS) is a line derived from Kansas random that has been selected for body weight for eight generations. The AR line was derived from the crossbreeding of Auburn and Rio Grande strains (A×R) followed by 6 generations of mass selection for body weight. Traits of this line include spawning late in the season. AR×MK was initiated by producing a 4-way crossbreed (Auburn × Rio Grande) × (Marion × Kansas) followed by 6 generations of mass selection; these fish are also late spawners. The Thompson strain originated from the Yazoo River, MS, and on-farm selection was conducted for several traits. including body size, disease resistance, and early spawning. The Tishomingo strain originated from the Tishomingo federal hatchery in Oklahoma. Kansas × Thompson (K×Th) was an F1 crossbreed between Kansas random females and Thompson males. Rio Grande is a single surviving wild female of a collection of 50 fish from the Rio Grande River, Texas. Traits of individuals of this strain collected 40 years ago included high dress-out percentage, susceptibility to disease, slow growth, large sexual dimorphism for body weight, high fecundity, small egg size, and maturity at two years of age. Strain mixing was initiated by the mixing of multiple strains.

The twelve blue catfish males (sires) were from four strains. These included Tombigbee (TBB), which originated from the Tombigbee River; Rio Grande (RG), which was from the Rio Grande River in Texas and has distinctive spots on the entire body; D&B, originating from D&B Fish Farms in Crockett, TX and were selected for small head size [42]; and D×R, an F1 crossbreed between D&B females and Rio Grande males.

2.2. Matings

Twenty channel catfish females were crossed with twelve blue catfish males following a North Carolina II factorial mating design due to its flexibility in producing unique interspecific hybrids from limited combinations of female channel catfish and male blue catfish coming from heterozygous crosses. Maternal half-sib, paternal half-sib, and full-sib families of F1 channel–blue hybrid catfish progeny were produced. However, due to the poor survival of some crosses, 40 families were obtained, resulting in an unbalanced design.

2.3. Spawning Procedures

Sexually mature male blue catfish with large muscular heads were selected and sacrificed. The testes were surgically excised and macerated in a 0.9% salt solution to produce sperm suspensions. The suspensions were stored in plastic tubes and refrigerated.

The females with the classic signs of readiness for spawning, including a soft, distended belly and a genital opening that is red and swollen [43,44], were selected for hormone-induced ovulation. These females were injected with luteinizing hormone analog (LHRHa) at 100 µg/kg via intraperitoneal implants and were placed in spawning bags (the same as ¼-inch mesh laundry bags) suspended in holding vats with flow-through water and aeration. The dissolved oxygen was maintained above 5 mg/L, and the water temperature was maintained at 26–30 °C. The females were checked for ovulation (presence of eggs released and sticking in their bags) about 36–72 h after hormone injection. Females that had ovulated were anesthetized with 100 parts per million (ppm) tricaine methane sulfonate (MS-222), rinsed with hatchery water, and dried with a towel. Through the application of abdominal pressure, the eggs were hand-stripped and placed into a stainless pan coated with vegetable oil to prevent the eggs from sticking to the pan. Eggs from each female were divided equally into aliquots based on the number of males for the factorial mating design and placed in a pan coated with vegetable oil. A sperm solution from each male was mixed with each aliquot of eggs. Hatchery water was then added to activate the fertilization. The fertilized egg masses were moved to a trough to allow them to water-harden for 15–20 min. After this, the eggs were moved to another trough with egg baskets and fry catchers. Fry catchers made of fine mesh nylon netting were used to prevent the newly hatched fry from escaping from the basket.

2.4. Fish Husbandry

After the eggs hatched, 210 fry from each family were stocked in three replicate 60 cm × 30 cm × 50 cm glass aquaria at a stocking density of 70 fry per aquarium with flow-through water and aeration. The water quality parameters were maintained at a flow rate of 4 L/minute, water temperature at 26–28 °C, and dissolved oxygen at >5 mg/L with the use of air diffusers. Each aquarium was labeled with the family information. The fry were initially fed the Purina® AquaMax® powdered starter diet containing 50% protein until they reached 2.5 cm in size. From 2.5–3.8 cm, the fish were fed a Purina® AquaMax® 100 diet containing 50% protein; from 3.8–5 cm, they were fed Purina® AquaMax® 200 containing 50% protein; and from 5–7.6 cm, they were fed Purina® AquaMax® 300 containing 50% protein. Fish were fed ad libitum daily. After 311 days of separate tank rearing in a flow-through system, all fish were injected individually with a PIT tag (model MiniHPT8, 8.4 mm, 132.2 kHz ISO FDX-B; Biomark, Boise, Idaho) into the mid-section of the abdomen.

For the next 245 days of rearing, 50% of the fish from each family, which were a total of 3108 fish, were stocked and reared in a communal 0.053 ha earthen split-pond system with an average depth of 1.5 m at 59,087 fish/ha. The remaining 50% of the fish from each family were kept in their original separate aquarium tanks, with a stocking density of 33 fish per tank. The flow-through aquarium system was then converted into a recirculating aquarium system to allow an additional 245 days of rearing of fish in separate tanks. The fish in separate tanks were fed with Purina® AquaMax® 300 containing 50% protein, while the fish in the communal split pond were fed ad libitum with 32% protein floating catfish pellets from Alabama Catfish Feedmill, Uniontown, AL, USA, LLC for 245 days.

Dissolved oxygen, ammonia, nitrite, pH, hardness, alkalinity, and temperature were monitored and recorded throughout the two phases of the experimental period. Water quality parameters were maintained at their optimum levels, whereas DO was >5 mg/L, ammonia was <1 mg/L, nitrite was <0.05 mg/L, pH was between 6 and 7, hardness was between 40 and 70 mg/L, and alkalinity was between 40 and 80 mg/L.

2.5. Data Gathering and Analyses

After 311 days of separate tank rearing in the flow-through system, data pertaining to early growth performance in terms of final mean body weight were gathered and recorded. Similar data were also measured after 245 days of additional tank rearing in the recirculating system and in the communal split-pond rearing. All data were analyzed to estimate the general and specific combining ability for the early growth performance of the hybrids in three different intensive rearing systems.

During the initial 311-day rearing period in the flow-through system, there was an early infection from *Aeromonas hydrophila* in the second month. The causative agent for this infection was confirmed to be the non-virulent strain (AL-01) of the *Aeromonas hydrophila* following PCR analysis of the putative *Aeromonas* isolates obtained from the moribund fish samples. This infection caused mortality across the hybrid families, which affected the actual weight of the fish. To account for this confounding density effect, the final body weight for flow-through system was adjusted using a regression coefficient before conducting statistical analyses following this formula:

$$\text{Adjusted Weight} = \text{Actual Weight} + [(\text{Initial Density} - \text{Final Density}) - \beta] \quad (1)$$

where β is the regression coefficient, which was found to be −0.16. Based on the results of the regression analysis, there was a significant negative linear relationship between the density and the weight, and the model fits the data. In fact, the Multiple R is 0.783, which indicated a strong linear relationship.

The statistical model we used as a genetic relationship matrix for the analysis of the early growth performance is stated below, as suggested by Becker [45] for factorial mating designs:

$$Y_{ijk} = \mu + S_i + D_j + (S \times D)_{ij} + e_{ijk} \quad (2)$$

where Y_{ijk} is the trait value for the kth hybrid progeny, μ is the overall mean, S_i is the random effect of the ith sire, D_j is the random effect of the jth dam, $(S \times D)_{ij}$ is the random effect of the cross between the ith sire and jth dam, and e_{ijk} is the random error.

The variance components are stated below following the genetic model II of Becker [45]:

$$\sigma^2_S = \text{cov}_{hs(S)} \quad (3)$$

$$\sigma^2_D = \text{cov}_{hs(D)} \quad (4)$$

$$\sigma^2_{SD} = \text{cov}_{fs} - (\text{cov}_{hs(S)} + \text{cov}_{hs(D)}) \quad (5)$$

$$\sigma^2_e = \sigma^2_T - \text{cov}_{fs} \quad (6)$$

where the variance components of sire (σ^2_S) and dam (σ^2_D) are equal to the covariance of half sibs (hs) of the sire groups and dam groups, respectively. The dam component also contains the maternal effect. The component for the cross (σ^2_{SD}) is the covariance of the full sibs (fs) minus the sum of the half sibs covariance from dams and sires. The variance for random error (σ^2_e) contains the remainder of the genetic variance and environmental variance.

Given that this experiment had unbalanced data with missing values for some crosses, the Restricted Estimation of Maximum Likelihood (REML) was used as the standard procedure to estimate the genetic variance components for random effects of sire, dam, and cross and the associated variance–covariance matrix. The missing data were assumed to be random. The Best Linear Unbiased Predictors (BLUP) of individual sires, dams, and cross, and their standard errors were generated with Mixed Procedure of SAS (version 9.4, SAS, Cary, NC, USA) to determine estimates of GCAs of sires, dams, and SCAs of crosses. All analyses were made at $p = 0.05$.

The strains of pooled parental sires, dams, or crosses from the more important genetic variance component were subjected to one-way analysis of variance using the GLM Procedure followed by the Tukey–Kramer Test to compare their performance means. The

Scheffé Test was performed for mean comparison with no significant difference results after Tukey–Kramer.

3. Results

The final mean body weights and phenotypic standard deviations of the forty hybrid catfish families in three different intensive rearing systems at two ages are presented in Table 1.

Table 1. The final mean body weights and phenotypic standard deviations (SD) of female channel catfish (*Ictalurus punctatus*) × male blue catfish (*I. furcatus*) F1 hybrid progeny in flow-through system for 311 days of separate tank rearing, recirculating system for an additional 245 days of separate tank rearing, and split-pond system for an additional 245 days of communal rearing.

Rearing System	Age (Days)	Final Mean Body Weight (g)	Phenotypic SD
Flow-through system (initial 311-day separate tank rearing)	311	8.07 g	1.79
Recirculating system (additional 245-day separate tank rearing)	556	91.25 g	36.21
Split-pond system (additional 245-day communal rearing)	556	194.21 g	94.07

The early growth performance in terms of final mean body weight was analyzed following REML/BLUP joint analyses based on the genetic relationship matrix to calculate the mean squares from the analyses of variance (Table 2), the variance components (Table 3), and the variance components ratio (Figure 1) and estimates for GCAs of sire and dam and/or SCAs of crosses (Figures 2–4). The mean comparison of parental strains after analyses of variance through GLM Procedure using Tukey–Kramer Test and Scheffé Test are presented in Figures 5 and 6.

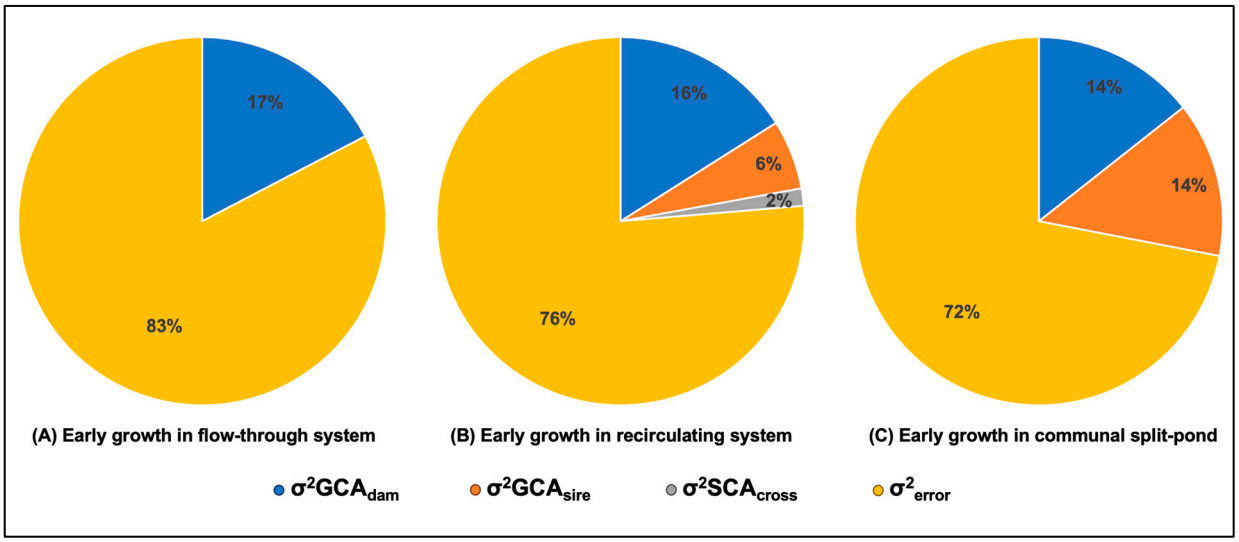

Figure 1. Ratio of estimates of GCA variance components for dam and sire, SCA variance components for cross, and error variance components for early growth in terms of final mean body weight of female channel catfish (*Ictalurus punctatus*) × male blue catfish (*I. furcatus*) F1 hybrid progeny in flow-through system for 311 days of separate tank rearing, recirculating system for an additional 245 days of separate tank rearing, and split-pond system for an additional 245 days of communal rearing.

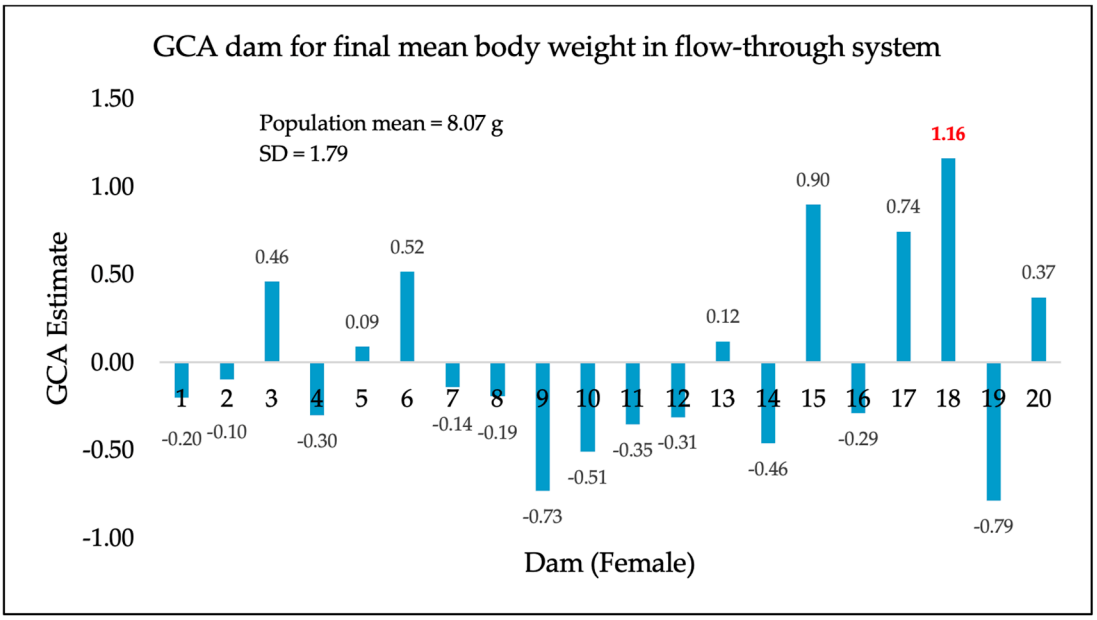

Figure 2. The channel catfish (*Ictalurus punctatus*) female (dam) general combining ability estimates for final mean body weight of female channel catfish (*I. punctatus*) × male blue catfish (*I. furcatus*) F1 hybrid progeny in flow-through system for 311 days of separate tank rearing. GCA estimates in red font are significantly different among others ($p < 0.05$, *t*-test). The strains of the dams are: A×R for Dam 9; AR×MK for Dam 10; KR for Dams 3–7; KS for Dam 8; K×Th for Dam 17; Mixed Strain for Dams 1, 18–20; RG for Dam 2; Thompson for Dam 16; and Tishomingo for Dams 11–15.

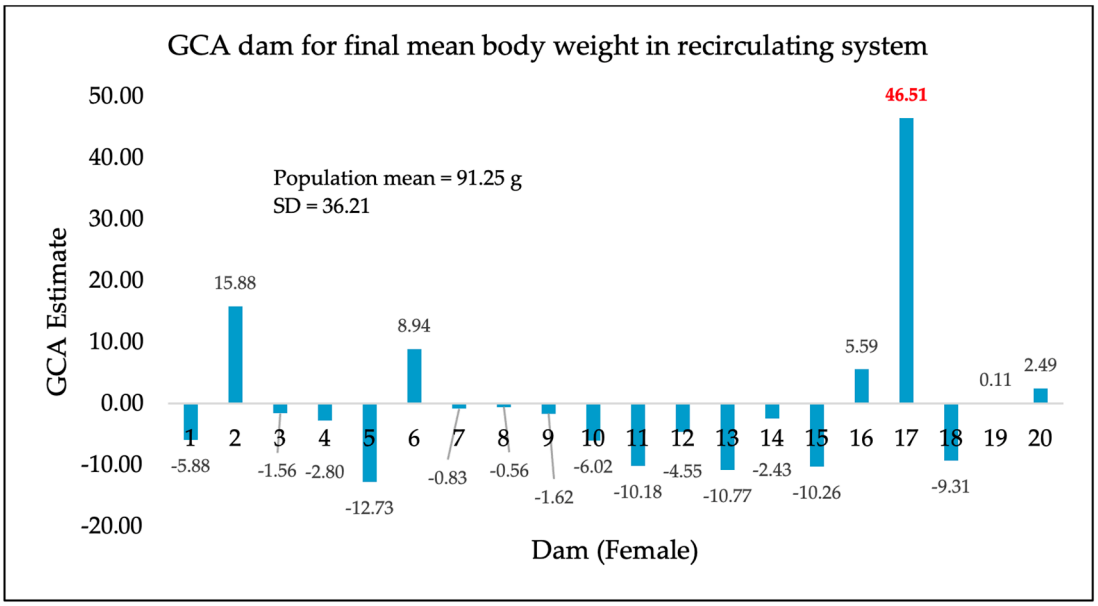

Figure 3. The channel catfish (*Ictalurus punctatus*) female (dam) general combining ability estimates for final mean body weight of female channel catfish (*I. punctatus*) × male blue catfish (*I. furcatus*) F1 hybrid progeny in recirculating system for an additional 245 days of separate tank rearing. GCA estimates in red font are significantly different among others ($p < 0.05$, *t*-test). The strains of the dams are: A×R for Dam 9; AR×MK for Dam 10; KR for Dams 3–7; KS for Dam 8; K×Th for Dam 17; Mixed Strain for Dams 1, 18–20; RG for Dam 2; Thompson for Dam 16; and Tishomingo for Dams 11–15.

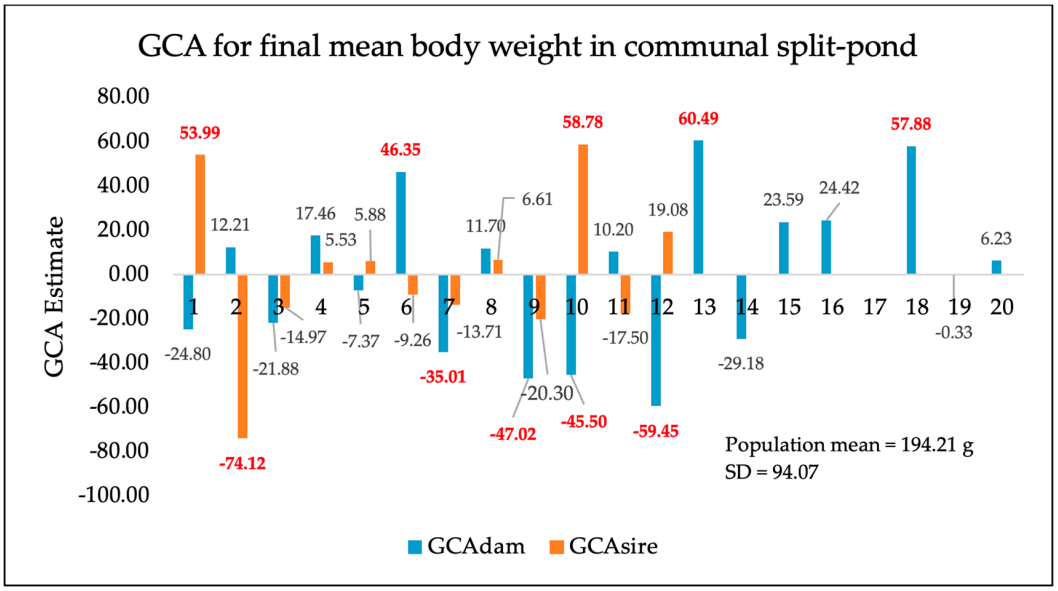

Figure 4. The channel catfish (*Ictalurus punctatus*) female (dam) and blue catfish (*I. furcatus*) male (sire) general combining ability estimates for final mean body weight of female channel catfish (*I. punctatus*) × male blue catfish (*I. furcatus*) F1 hybrid progeny in split-pond system for an additional 245 days of communal rearing. GCA estimates in red font are significantly different among others ($p < 0.05$, *t*-test). The strains of the dams are: A×R for Dam 9; AR×MK for Dam 10; KR for Dams 3–7; KS for Dam 8; K×Th for Dam 17; Mixed Strain for Dams 1, 18–20; RG for Dam 2; Thompson for Dam 16; and Tishomingo for Dams 11–15. The strains of the sires are: DB for Sires 2, 4–9; D×R for Sires 1 and 10; RG for Sires 15 and 16; and TBB for Sire 3.

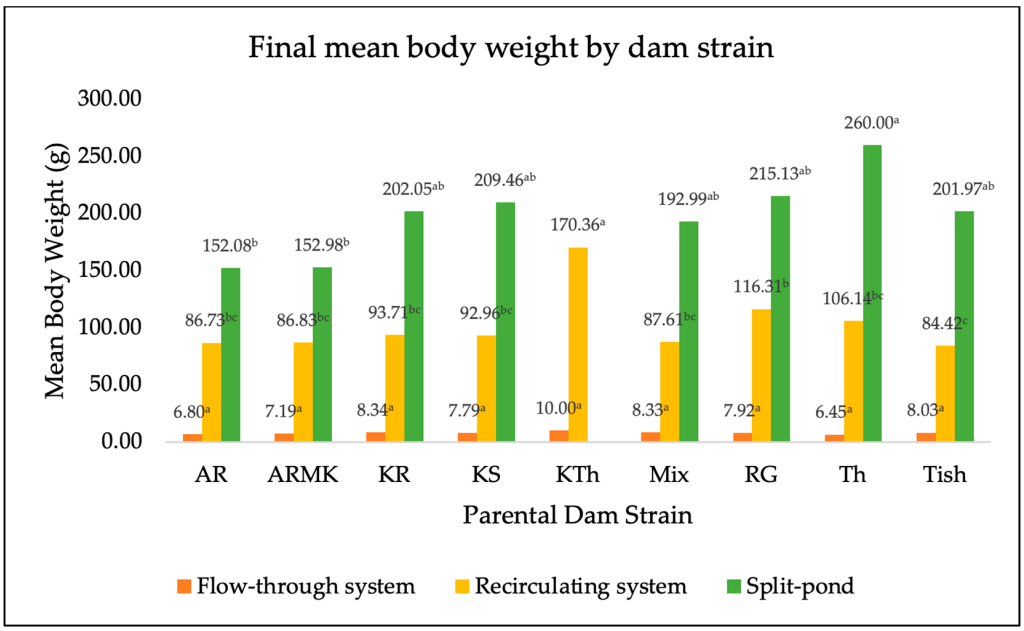

Figure 5. Final mean body weight by parental dam strain of female channel catfish (*Ictalurus punctatus*) × male blue catfish (*I. furcatus*) F1 hybrid progeny in flow-through system for 311 days of separate tank rearing, recirculating system for an additional 245 days of separate tank rearing, and split-pond system for an additional 245 days of communal rearing. Hybrid genotypes in the same rearing system from parental dam strains with the same superscript letter are not significantly different ($p > 0.05$, Tukey–Kramer Test). For genetic types in the communal split-pond, the mean comparison was performed following the Scheffé Test.

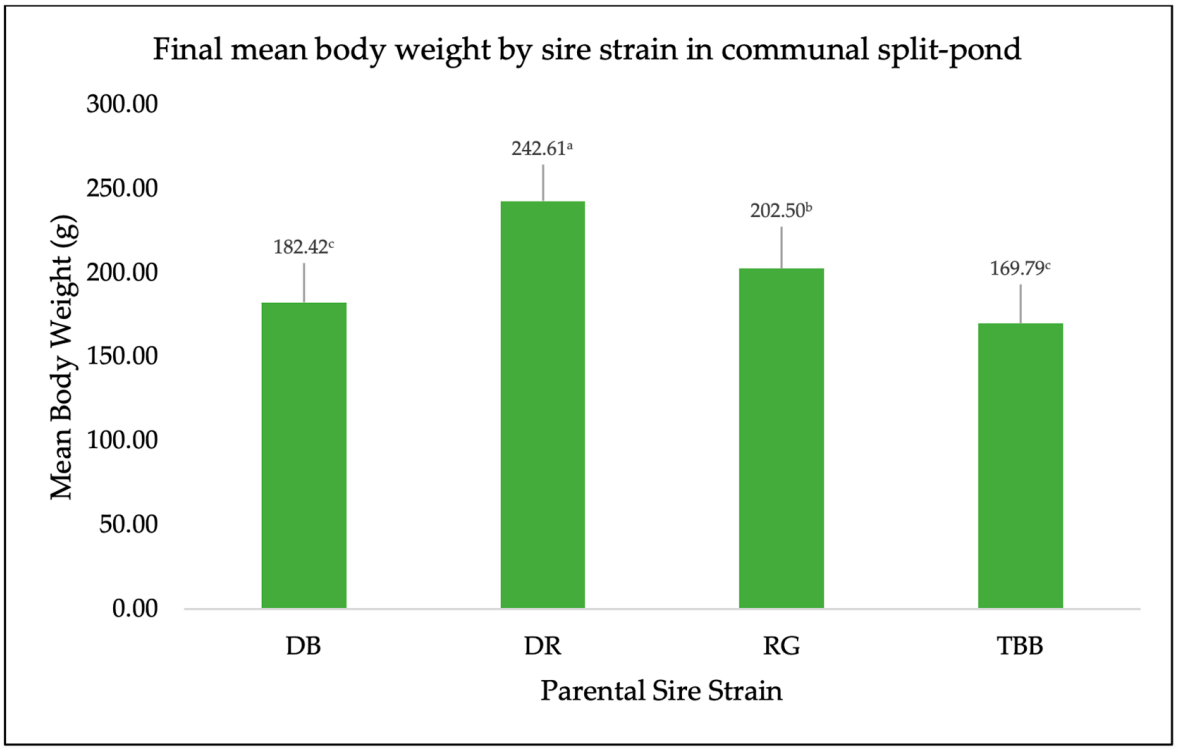

Figure 6. Final mean body weight by parental sire strain of female channel catfish (*Ictalurus punctatus*) × male blue catfish (*I. furcatus*) F1 hybrid progeny in split-pond system for an additional 245 days of communal rearing. Hybrid genotypes from parental sire strains with the same superscript letter are not significantly different ($p > 0.05$, Scheffé Test).

In all three intensive rearing systems, significant differences were observed in the mean squares of hybrid progeny for the final mean body weight ($p < 0.05$, Table 2). This indicated significant effects from family, dam, sire, and sometimes interactions.

Table 2. Mean squares (MS) from Type 3 Mixed Procedure for final mean body weight of female channel catfish (*Ictalurus punctatus*) × male blue catfish (*I. furcatus*) F1 hybrid progeny in flow-through system for 311 days of separate tank rearing, recirculating system for an additional 245 days of separate tank rearing, and split-pond system for an additional 245 days of communal rearing.

Rearing System	Age (Days)	Source of Variation			
		Dam (d.f.)	Sire (d.f.)	Dam × Sire (d.f.)	Error MS (d.f.)
Flow-through system (initial 311-day separate tank rearing)	311	4.81 * (19)	1.72 ^{ns} (11)	3.28 ^{ns} (8)	2.78 (65)
Recirculating system (additional 245-day separate tank rearing)	556	5059.56 * (19)	3028.11 * (11)	908.11 ^{ns} (8)	1064.29 (677)
Split-pond system (additional 245-day communal rearing)	556	66867 * (18)	85175 * (11)	7699.88 ^{ns} (7)	7315.98 (1480)

After ANOVA *F*-test: * = $p < 0.05$, and ^{ns} = $p > 0.05$; d.f. = degree of freedom.

Table 3. Estimates of general combining ability variance for dam (σ^2GCA_d) and sire (σ^2GCA_s) and specific combining ability variance (σ^2SCA), error variance (σ^2E) and corresponding standard errors for final mean body weight of female channel catfish (*Ictalurus punctatus*) × male blue catfish (*I. furcatus*) F1 hybrid progeny in flow-through system for 311 days of separate tank rearing, recirculating system for an additional 245 days of separate tank rearing, and split-pond system for an additional 245 days of communal rearing.

Rearing System	Age (Days)	Genetic Parameter Estimates			
		σ^2GCAd (±SE)	σ^2GCAs (±SE)	σ^2SCA (±SE)	σ^2E
Flow-through system (initial 311-day separate tank rearing)	311	0.57 (0.37)	0	0	2.68
Recirculating system (additional 245-day separate tank rearing)	556	222.83 (124.68)	85.43 (68.21)	20.7 (56.32)	1060.16
Split-pond system (additional 245-day communal rearing)	556	1463.21 (587.61)	1388.25 (663.43)	0	7322.73

Following the initial 311-day separate tank rearing of the hybrids in a flow-through system, the GCA effect of the dam for the final mean body weight was significant ($p < 0.05$), and the largest component for this trait was the GCA variance for the dam (Table 3, Figure 1). This highlighted the importance of additive gene action for early growth.

The GCA effects of the dam showed that Parent 18 significantly had the highest positive GCA estimates of 1.16 for final mean body weight ($p < 0.05$, Figure 2). This suggests that its progeny would likely exhibit superior early growth performance when reared in separate tanks in a flow-through system.

Although no significant differences were found among the strains of the dam for the final mean body weight ($p > 0.05$, Figure 3), the hybrid progeny of K×Th crossbred dams had the highest value (10.00 g) compared to all other dam genotypes in the flow-through system.

After an additional 245-day period of separate tank rearing in the recirculating system, the GCA effects of both dam and sire parents on the final mean body weight were found to be significant ($p < 0.05$, Table 2). The ratio of the combining ability variance components indicated that the largest component was the GCA variance for the dam (Table 3, Figure 1), suggesting that early growth was primarily controlled by the additive gene action of the dam parents.

Parent 17 stood out among the dams, providing the highest GCA estimate for final mean body weight at 46.51 ($p < 0.05$, Figure 3). This suggests that Parent 17 is a superior combiner, likely to produce hybrid progeny with better early growth performance compared to other dams.

The hybrid progeny of the K×Th crossbred dam strain had the highest early growth with 170.36 g ($p < 0.05$, Figure 5), followed by the RG hybrid type. However, the RG hybrid type did not significantly differ from all other dam strains ($p > 0.05$, Figure 5).

After an additional 245-day period of rearing hybrid catfish in a communal split-pond, the GCA effects of both male and female parents on the final mean body weight were found to be significant ($p < 0.05$, Table 2). The ratio of the variance components of combining ability (Table 3, Figure 1) indicated that the largest additive gene actions controlling the early growth were attributed almost equally to both dam and sire parents.

Among the dams, parents 13, 18, and 6 stood out with the highest positive GCA estimates for final mean body weight at 60.49, 57.88, and 46.35, respectively ($p < 0.05$, Figure 4). Similarly, among the sires, parents 10 and 1 had the highest positive GCA estimates at 58.78 and 53.99, respectively ($p < 0.05$, Figure 4). This suggests that these

parental dams and sires would likely produce hybrid progeny with superior early growth performance when reared in communal split-pond.

With respect to parental dam strains, the hybrids from Thompson dams had the highest with 260.00 g final mean body weight (Figure 3), while A×R and AR×MK hybrids had the lowest values. For the parental sire strains, the hybrids from D×R crossbred sires had the highest at 242.61 g (Figure 6), followed by the RG hybrids, while the TBB and DB hybrids were the lowest in the communal split pond.

4. Discussion

The application of hybrid catfish is increasingly prevalent due to their faster growth rate, better survival rate, disease resistance, tolerance of low oxygen, carcass yield, and seinability. However, hybrid catfish performance could be further improved through reciprocal recurrent selection if GCA and/or SCA are of sufficient magnitude. In the current study, dam GCA had the strongest influence on early growth (body weight) in aquaria. As the fish grew larger, the percentage of variance due to genetics gradually increased, and after the hybrid progeny were transferred to ponds, the dam and sire GCAs equalized.

Bosworth and Waldbieser [26] estimated the GCA and SCA variances for growth and carcass yield [40] in market-sized hybrid catfish. The dam GCA for body weight was the strongest factor. However, when maternal effects are accounted for, the dam and sire GCAs were likely equivalent. In the current study, dam GCA had the strongest influence on early growth (body weight) in aquaria, especially at the initial stage in the flow-through system. SCA was not detectable at this time. The relative influence of dam additive gene effects, sire additive gene effects, and dominance changed across the three evaluated environments or time points. This suggests either genotype–environment interactions or genotype–age interactions. In the study conducted by Bosworth and Waldbieser [26], the pond environment, which had fish more similar in size to the experimental group, yielded nearly identical results, showing an equivalence of sire and dam GCAs. However, one notable difference may be the presence of more maternal effects in their study.

The similarity in the results for body weight between the current study and that of Bosworth and Waldbieser [26] is significant. They utilized different strains than the current study, which suggests that the genetics of variable hybrid performance are similar across different strains and lines of channel catfish and blue catfish. Thus, a standard breeding program to improve the growth rate of hybrid catfish should be applicable industry-wide.

Our results and those of Bosworth and Waldbieser [26] indicate that when hybrid progenies are evaluated in ponds, selection for channel catfish female and blue catfish male body weight should result in faster-growing hybrid progeny. After four generations of selection for body weight in the Kansas strain of channel catfish, the initial prediction was not accurate [46]. Hybrids from control females grew at the same rate as hybrids from selected females. However, after eight generations of selection for body weight in the Kansas strain, the prediction became accurate. Hybrid fingerlings from selected females grew faster than hybrids from control females [47,48]. The explanation for the change over a four-generation period is not clear; however, allele frequency changes would be expected between generations, and this could explain the variable results as additive genetic variation and genetic correlations can change over generations. The dam GCA suggests that the selection of channel catfish females for body weight should result in faster-growing hybrids, and this will need to be verified in multiple populations to determine the generality of this prediction.

The type of gene action changed over time or by environment, suggesting that genetic ranking stayed the same and genotype–environment interactions were minimal. However, this conclusion is not correct. If the dam GCA of individual females is examined, the ranking of the females with the highest GCA changes for different environments or age/size of the progeny. Thus, strong genotype–environment or genotype–age interactions occurred, or

both. Additionally, the selection of the female brood stock is affected by the environment and age/size of the hybrid progeny.

For two of three environments or final sizes of progeny assessed in this study, the GCA variance of the parental dams was larger than the GCA variance of the parental sires and the SCA variance. Several studies on fish species such as hybrid catfish [26,39,40], hybrid striped bass (*Morone chrysops* × *Morone saxatilis*) [35], sea bass (*Dicentrarchus labrax* L.) [34], and carp (*Cyprinus carpio* L.) [33] that analyzed factorial matings also revealed larger additive variance (GCA) than the dominance variance (SCA).

Bosworth and Waldbieser [26] found that genetic variance in female channel catfish led to a higher degree of additive variance, as evidenced by microsatellite data showing high polymorphism. These females were a mix of different strains from commercial farms with large breeding populations, hence the expected high polymorphism. In contrast, the blue catfish used, sourced from a single strain from a commercial farm, showed low polymorphism, leading to less additive variance. The assumption here is that additive variation quantity correlates with microsatellite variation quantity. However, microsatellites do not differentiate between additive and dominant genes and expression. Therefore, using a population from many strains could result in significant dominance effects, increasing the SCA impact. Even in highly inbred lines, significant additive variation can exist [49], making GCA important even with limited microsatellite variability.

In the current study, the genetic variance could not be attributed solely to the partitioning of genetic components for the above reasons and because high polymorphism effects were expected in both male and female catfish parents used. The female parents were a mix of lines and a crossbreed of channel catfish, suggesting a highly polymorphic overall female population. The male blue catfish, comprising three strains and a crossbreed, could also result in high polymorphism. However, their microsatellite markers indicated relatively low genetic variability [50].

In this study, GCA was the strongest genetic component explaining the genetic variation for growth under the three conditions and life stages. Parents with higher GCA estimates should generate progeny with the highest mean yield, from which elite parental lines can be selected. However, inbreeding should be avoided when developing these lines as reproductive output could be greatly decreased. The GCA performance of these parental lines can be predicted from the GCAs of their parents because the GCA is controlled by the additive gene effects, which are heritable from the parents and can be passed onto the progeny [51]. Hence, the improvement of the hybrid catfish becomes effective and less costly due to the lower time taken to release F1 hybrids with a low amount of materials needed in the breeding programs.

As this study was conducted on young, small hybrid catfish and stocker-sized catfish, future research should confirm the relationship between the genetic mechanisms we found and that of food-size hybrid catfish to ensure that the research has practical application not only to fingerling producers but also food fish producers. Genotype–environment interactions should also be further explored. Future research could also involve integrating molecular aspects of combining ability. Linkage analysis on both the GCA and SCA effects for each trait could also be conducted to explore and unveil the QTLs of combining abilities for important traits and evaluate how they contribute to the overall performance of hybrid catfish.

5. Conclusions

The early growth of the F1 hybrid catfish was found to be controlled by the additive gene action attributed to the parental channel catfish females when hybrids were reared in aquaria to fingerling size. However, the additive gene action from both parental channel catfish females and blue catfish males equalized when hybrids were reared in the earthen pond environment and at an advanced stocker size. There were genotype–environment interactions affecting the combining abilities, both the amount and the type of genetic variation.

A breeding plan can be developed to improve the early growth of F1 channel–blue hybrid catfish utilizing GCA and SCA information from this study. Using the GCA/SCA estimates obtained from the analyses of combining ability, elite parental and/or cross genotypes capable of producing superior hybrid catfish were identified, and performance of hybrid catfish progeny could be predicted. The genetic mechanisms observed should allow reciprocal recurrent selection of channel catfish and blue catfish to develop high-yielding parental lines and hybrids that would be beneficial to the catfish industry.

Author Contributions: R.O. and R.D. conceived and designed the experiment and analyzed the results; R.O., A.E., K.K., K.V., N.J.C.B., Z.T. and D.D. executed the experiments; R.O., A.E., K.K., K.V., N.J.C.B., Z.T., D.R., W.S.B., D.C., K.G., Z.Y. and G.Q. collected the samples, gathered data, and performed the fish care; R.O. conducted the statistical analyses; R.O. and R.D. wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: The study was conducted in accordance with the Declaration of Helsinki, approved by the Auburn University Institutional Animal Care and Use Committee (AUIACUC; Protocol Review Number: 2016-2871; Approval date: 14 April 2016), and followed the Association for Assessment and Accreditation of Laboratory Animal Care protocols and guidelines.

Data Availability Statement: Data are contained within the article.

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Conflicts of Interest: The authors declare that they have no conflicts of interest.

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